AN EXTINCT 'SWAN-GOOSE' FROM THE PLEISTOCENE OF MALTA

by E. MARJORIE NORTHCOTE

ABSTRACT. Qualitative and quantitative studies on extinct *Cygnus equitum/Anser equitum* from the Ipswichian (Eemian) Interglacial of Malta (*c.* 125 000 B.P.) show it was a broad-bodied, dwarf swan with some goose-like features. It was closer to Whooper and Bewick's *C. cygnus* than Mute Swans *C. olor* though the relative shortness of the chief hand bones resembles the latter. Feathered wing span was *c.* 1·5 m. The wings were probably more 'elliptical' than in other swans; 'stouter' carpometacarpus and ulna(?) suggest higher camber and relatively shorter hand bones suggest lower aspect ratio (length:width) than in Whooper Swans. There is no evidence to support assertions that it was flightless. The wings were fully feathered, it was light enough (*c.* 3·5–4·0 kg) to fly and the flight apparatus was not reduced. The femur was comparatively 'stout'. Abundant on the island, *C. equitum* may have swum on fresh and brackish water, walked well and, unlike other swans, have habitually taken off and alighted on land. It probably ate highly calorific plant food in enclosed, rather terrestrial habitats. Morphological differentiation facilitated coexistence with Whooper Swan and the giant, flightless, extinct swan *C. falconeri*. The two extinct, more advanced swans probably arose from the same fully flighted stock as Whooper Swans.

BATE (1916) based *Cygnus equitum* on fossils of what she considered to be a small extinct swan and Lambrecht (1933) and Howard (1964) agreed but Brodkorb (1964) named them *Anser equitum* (Bate), an extinct goose. Bate (1916) briefly described and figured the holotype (a carpometacarpus) and paratypes (a proximal humerus and a coracoideum) of *equitum* and mentioned fragments, now lost, of two ulnae and a radius, all from Pleistocene deposits at Ghar Dalam, Malta.

This, the first detailed study on *equitum*, aims to ascertain the genus and affinities of the bird, to suggest its probable size, form, and habitat and to investigate its habit, particularly with respect to Bate's (1916) claim that *equitum* was flightless.

AGE OF THE FOSSILS

In Ghar Dalam cavern the *equitum* type series lay in red earth matrix (Bate 1916), characteristic of the bone-bearing stratum of Maltese caves and fissures. The stratum is thin so Adams (1870) and de Bruijn (1966) considered all the bones were deposited in a short time span and represent one faunal sample. The matrix is highly calciferous. No countable pollen for dating has been found (Zammit-Maempel 1982; Northcote 1982*a*); indeed no precise dates are available for the sediments or fauna (Pedley 1981, p. 71). At times during the Pleistocene, Sicily and Malta were connected by an isthmus or island chain with sea-level lower than at present (Zammit-Maempel 1977; Sondaar and Boekschoten 1967). Bones of *equitum* were associated with extinct pygmy elephant *Palaeoloxodon melitensis* (Falconer, 1862), that flourished on Siculo-Malta in a period equivalent to the Ipswichian (Eemian) Interglacial Stage of more northern countries (Sondaar 1971), 114 000–135 000 years ago (Gascoyne *et al.* 1983). This then, may also be taken as the date of *equitum*.

SPECIMENS, METHODS, AND TERMINOLOGY

The type series of *C. equitum* Bate, 1916 is in the National Museum of Natural History, Malta (Specimens NMM 20 and 21). Casts, catalogued *A. equitum* (Bate) are in the British Museum (Natural History), London (Specimens BMNHL A1613, 1614, 1615). From Maltese Pleistocene anseriform fossils, unidentified or identified as *C. falconeri* Parker, 1865 or *C. equitum*, in those museums and the University Museum of Zoology, Cambridge (UMZC) I chose specimens consistent with the *equitum* types. Reference skeletons

include Greylag *A. anser*, White-fronted *A. albifrons*, Barnacle *Branta leucopsis* and Brent Geese *B. bernicla*, and Whooper and Bewick's *C. cygnus* and Mute Swans *C. olor* from the following: University Museum of Zoology, Cambridge, Sedgwick Museum, Cambridge (SMC), BMNH, Tring (BMNHT), Royal Scottish Museum, Edinburgh (RSM), Glasgow Museum (GM), Leicester Museum (LM), and Colchester and Essex Museum (CEM).

I chiefly use *Anser* (less specialized than *Branta*, Johnsgard 1965), in particular Greylag Goose (the largest western Palaearctic goose, Cramp and Simmons 1977) for comparisons with geese. I follow Johnsgard (1974) in treating Whooper and Bewick's Swans as elastically similar Eurasian subspecies of *C. cygnus*. Because of their more southern Palaearctic distribution, I chiefly use Whooper *C. c. cygnus* and Mute Swans for comparison with swans.

I follow Verheyen (1953, 1955), Simpson *et al.* (1960), and Woolfenden (1961) who used ratios for mensurational comparison. For comparing 'stoutness', where accurate measurements are obtainable, viz. humerus and carpometacarpus, I follow Kuhry and Marcus (1977) and compare logarithms of ratios. Weight predictions are made using scaling formulae. Following Scott (1983) they are based on several parameters within similar morphological groups. For estimating *equitum* weight, I use the humerus and femur (the bones least likely to be modified by habit, Bellairs and Jenkin 1960).

Methods of preparation and measurement are given elsewhere (Northcote 1979*a*, *b*, 1982*a*). Many of the distinctions between Anserini cited follow Woolfenden (1961). Taxonomy follows Delacour (1954) and Johnsgard (1974). Anatomical nomenclature follows Baumel (1979) and Vanden Berge (1979).

QUALITATIVE CHARACTERS

Cranium

Specimen BMNHL A3267 (text-fig. 1) comprises the frontal area with right supraorbital margin, postorbital region and occipital plane with condyle, foramen magnum, and alae tympanicae. Specimen UMZC 252*a* comprises a braincase infill with a posterior frontal bone fragment attached to an occipital plane with dorsoventrally compressed condyle and foramen magnum.

The sulcus gl. nasalis in *equitum* resembles certain geese and extant northern swans in being comparatively extensive (text-fig. 1*a*–*c*). However, the *equitum* cranium differs from geese, but is like swans, as follows: 1, the foramen n. olfactorii et sulcus olfactorius are overarched with bone (Shufeldt 1909); 2, the proc. postorbitalis is enlarged rostrally and directed more ventrally (text-fig. 1*d*–*f*); 3, the crista temporalis forms a distinct ridge, and the fossa temporalis is large and distinct (text-fig. 1*h*–*j*); 4, the crista nuchalis transversa forms a distinct ridge demarcating the occipital plane (text-fig. 1*g*–*l*); and, 5, occipital fontanelles are absent (Stejneger 1882) (text-fig. 1*g*–*l*). There is no indication in the extinct bird of the bony frontal bill knob diagnostic of Mute Swans (text-fig. 1*b*).

In *equitum* the large sulcus for the glandula nasalis (salt gland) suggests that it could live near estuaries or the sea (Holmes and Phillips 1985). The other cranial characters indicate the comparatively larger ligaments and muscles of a longer swan-like beak.

EXPLANATION OF PLATE 69

Figs. 1, 4, 7, goose; 2, 5, 8*a*–*c*, *equitum* (BMNHL A5218, 5221, 5222, 5186, respectively); 3, 6, 9, Whooper Swan.

Figs. 1–3. Scapula, lateral surface of cranial extremity showing acromion (F).

Figs. 4–6. Coracoideum, dorsal aspect of cranial extremity showing area (G) between proc. procoracoideus and acrocoracoideus.

Figs. 7–9. Humerus. *a*, caudal surface of proximal extremity showing caput humeri (H), tuberculum ventrale (I), fossa pneumotricipitalis (J), margo caudalis (K), incipient second fossa pneumotricipitalis (L), crista pectoralis (m), impressio m. supracoracoidei (N), tuberculum dorsale (O). *b*, caudal surface of distal extremity showing fossa olecrani and sulci m. humerotricipitis and scapulotricipitis (P). *c*, cranial surface of distal extremity showing fossa m. brachialis (Q).

All magn. × 1.

PLATE 69

NORTHCOTE, goose, swan, and swan-goose
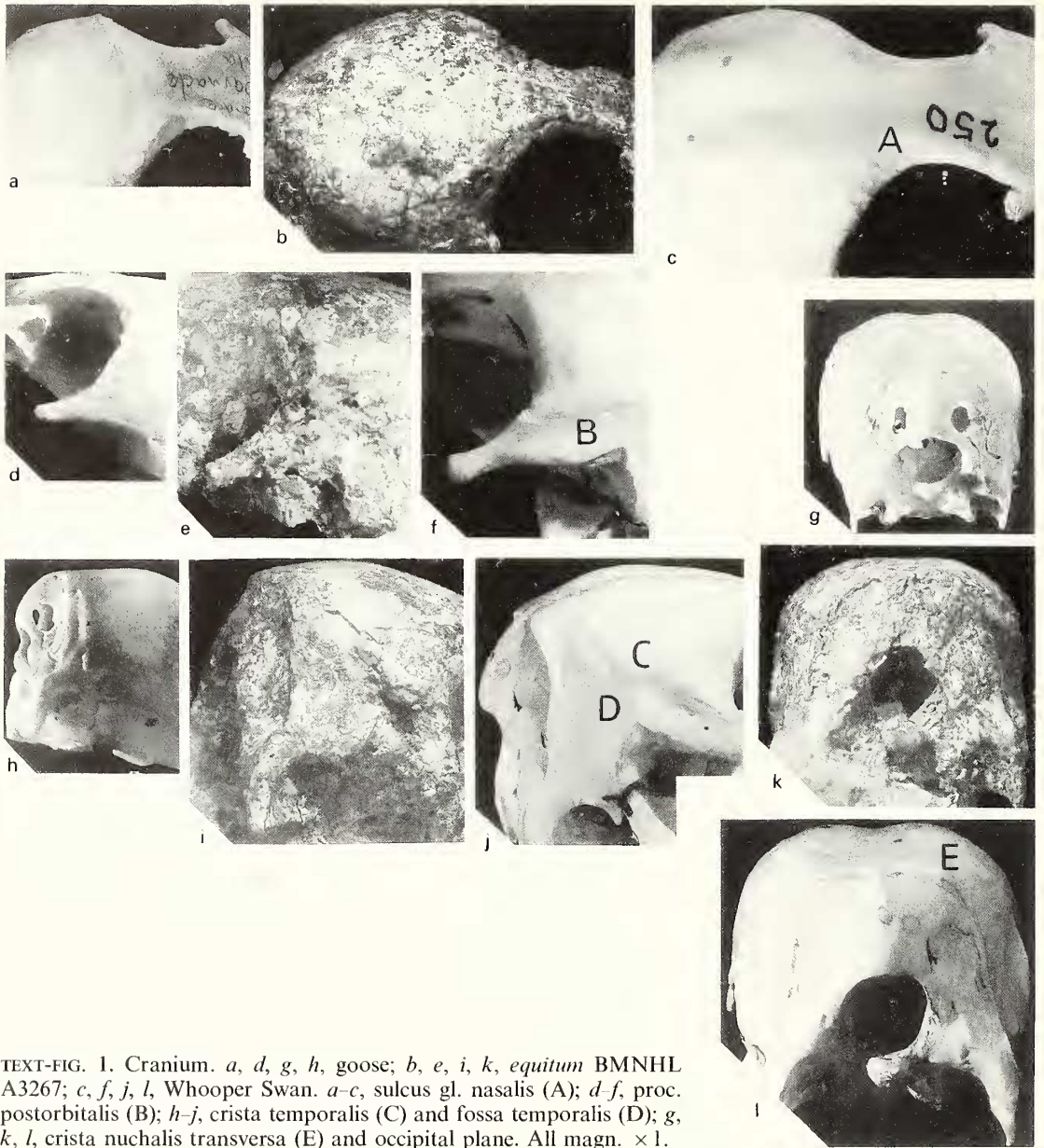
TEXT-FIG. 1. Cranium. *a, d, g, h*, goose; *b, e, i, k, equitum* BMNHL A3267; *c, f, j, l*, Whooper Swan. *a–c*, sulcus gl. nasalis (A); *d–f*, proc. postorbitalis (B); *h–j*, crista temporalis (C) and fossa temporalis (D); *g, k, l*, crista nuchalis transversa (E) and occipital plane. All magn. ×1.

Scapula and coracoideum

The *equitum* scapula differs from geese, but resembles swans, in lacking a pneumatic foramen laterally between the acromion (that is cranially attenuated) and the facies artic. humeralis (Pl. 69, figs. 1–3). The *equitum* coracoid differs from geese but resembles swans as follows: 1, the area between the proc. procoracoideus and acrocoracoideus is flat (Pl. 69, figs. 4–6); and, 2, numerous small pneumatic foramina occur under the entire edge of the facies artic. clavicularis; in geese there is only one large hole.

In swans, absence of a scapular air sac may facilitate upending, and in *equitum* its similar absence may indicate a similar habit.

Humerus

Proximally, the *equitum* humerus differs from geese but resembles swans as follows: 1, the tuberculum ventrale is less attenuated; and 2, there is an incipient second (dorsal) fossa pneumotricipitalis (an advanced character, Bock 1962) bordered by a ridged margo caudalis (Pl. 69, figs. 7*a*–9*a*) (Bate, 1916 considered that *equitum* had a single deep fossa). In one character, the *equitum* humerus resembles geese; at the cranial end of the crista pectoralis there is an impressio m. supracoracoidei forming a caudal lip on the tuberculum dorsale. As Bate (1916, p. 430) observed of *equitum*, 'the general outline is squarer' than in swans (Pl. 69, figs. 7*a*–9*a*). Distally, the *equitum* humerus differs from extant swans and geese: 1, the fossa olecrani is much shallower, and the sulci m. humerotricipitalis and scapulotricipitalis are much deeper (Pl. 69, figs. 7*b*–9*b*); and, 2, the fossa m. brachialis is deeply excavated and oval-shaped (Pl. 69, figs. 7*c*–9*c*).

The *equitum* humerus differs from Mute, but resembles Whooper, Swans: 1, the m. latissimi dorsi insertion is clearly marked on the caudal shaft surface and turns ventrally below the caput humeri; in Mute Swans the line is indefinite and straight; and, 2 insertion of the m. scapulohumeralis in the fossa pneumotricipitalis is poorly marked and lacks a raised border; in Mute Swans it is clearly marked and bordered.

The supracoracoideus muscle that inserts on the crista pectoralis and on the tuberculum dorsale and impressio m. supracoracoidei (when present) (Baumel 1979) is essential for take-off from level ground (Sy 1936), and most highly developed in birds specialized for slow flapping flight and jump take-offs (Pennycuick 1972). Swans usually take off and land on water by pushing the water with their feet (Cramp and Simmons 1977); their lack (atrophy?) of an impressio m. supracoracoidei may be correlated with this habit. Greylag Geese, like other large geese, more frequently perform jump take-offs and land on level ground using their wings (Cramp and Simmons 1977); the presence of an impressio m. supracoracoidei in them may be correlated with this habit and the same may apply to *equitum*. The differences between *equitum* and recent Anserini in both fossa olecrani and fossa m. brachialis suggest differences in elbow flexion, and, therefore in lift mechanisms.

Antebrachium

I can find no difference in radius or ulna between *equitum* and recent Anserini. Bate (1916) stated the *equitum* ulna lacked papillae remigiales caudales, but ulnae such as BMNHL A5225 (Pl. 70, fig. 1) bear papillae. Bate's (1916) specimen may have been eroded. Contrary to Brodkorb (1964), the *equitum* carpometacarpus resembles swans, rather than geese: 1, the proximal articulatory surface is almost flat (Pl. 70, figs. 2*a*–4*a*); Bate (1916) erroneously considered it even flatter than in swans; 2, the proc. extensorius of the os metacarp. alulare is less attenuated and the angle between this process and the trochlea carpalis is larger (Pl. 70, figs. 2*b*–4*b*); and, 3, the dorsal rim of the facies artic. dig. major forms an arc. According to Bate (1916, p. 429), in *equitum* the os metacarpale minus and major separate 'for a comparatively much shorter distance (than in a recent swan) causing the articular ends to be more massive'. On the holotype (as on other specimens) only the minus ends remain so there is no evidence for her statement. Like the ulna, the metacarpale majus of *equitum* bears feather papillae (Pl. 70, fig. 3*c*). The phalanx proximalis digiti majoris of the *equitum* manus resembles swans in having a discrete proximodistal ridge between two grooves (Pl. 70, figs. 5–7).

Papillae remigiales caudales on ulna and carpometacarpus indicate that *equitum* had the chief flight feathers. The flatter proximal surface and rounder rim of the facies artic. dig. major in *equitum* and swans may be related to the shape and disposition of the proc. extensorius of the os metacarp. alulare (concerned with muscles extending the hand and keeping taut the propatagial skin fold, George and Berger 1966) and indicate greater rotation at wrist and major digit in *equitum* and swans than in geese. Tendons of muscles that control wing-tip movement cross the proximal phalanx and insert on the second phalanx of the dig. majoris (George and Berger 1966). In geese,

there is a certain amount of play of the tip, but in swans the tendons are constrained by the ridge and its flanking grooves on the proximal phalanx with, consequently, less play. This must also have been the condition in *equitum*. All these similarities in form of wrist and hand bone in *equitum* and swans suggest similar use of the wing tip, e.g. during wing-tip reversal for fast speed (Brown 1963).

Hind limb bones

A femur shaft NMM F.22, No. 31 reported by Despott (1928/1929), combined with the extremity BMNHL A5812, represents an *equitum* right femur. Compared to geese, the trochlea fibularis and condylus lateralis flare less laterally in *equitum* and swans (Pl. 70, figs. 8–10). A distal *equitum* tibiotarsus NMM No. 26, reported by Despott (1928/1929) has pons supratendineus, canalis extensorius, and incisura intercondylaris, but damaged condyles. An *equitum* tarsometatarsus fragment (BMNHL A5810) is a distal shaft with trochlea of metatarsals III and IV enclosing the incisura intertrochlearis lateralis and typical anserine bridge. In geese and *equitum*, but not swans, the trochlear groove of metatarsal IV has a proximodistal swelling (Pl. 70, figs. 11–13).

In resembling geese rather than swans, the *equitum* leg-bone characters suggest that, like the former, the extinct bird walked efficiently and may contribute evidence that *equitum* habitually took off and landed on level ground.

QUANTITATIVE CHARACTERS

'Stoutness'

On the *equitum* coracoid dorsoventral width at the cotyla scapularis is 19·9–22·2 % of length; this is above the range for geese (15·0–17·6 %) but like that for swans (16·4–22·1 %). For the *equitum* coracoid shaft, range for ratio (width : length) is approx. 0·152–0·161; for Mute Swan UMZC 249 it is approx. 0·141 and for Whooper Swan UMZC 250 and Bewick's Swan UMZC P6 approx. 0·158 and 0·159, respectively. Thus the *equitum* shaft, though relatively wider than in the Mute Swan, is, contrary to Bate (1916), not wider than in the Whooper Swan. For Greylag Geese SMC 533–544 and BMNHT 1852.2.20.10, this ratio is approx. 0·138. Bate (1916) also stated the *equitum* coracoid has greater mediolateral facies artic. clavicularis width than a swan. However, in the fossils the faeies edge is eroded.

Limb-bone measurements of *equitum*, Greylag Geese, and extant Palaearctic swans are given in appendices 1 and 2 (lodged in the British Lending Library, no. 14035), means in Table 1. $\log_{10}$ (ratio width : length) for *equitum* and Whooper Swan humeri do not significantly differ (95 % level; $P > 0.05$). Whooper Swan humeri are significantly 'stouter' than Mute Swan humeri ($P < 0.001$, Northcote 1981), hence *equitum* humeri also are significantly 'stouter'. However, *equitum* humeri are significantly less 'stout' ($P < 0.05$) than those of Greylag Geese. The ratio (width : length) for two *equitum* ulnae (approx. 0·042) is less than in Greylag Geese (0·051), but greater than in Whooper and Mute Swans (0·039 and 0·038, respectively). $\log_{10}$ (ratio width : length) comparisons for the

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EXPLANATION OF PLATE 70

Figs. 2, 5, 8, 11, goose; 1, 3, 6, 9, 12, *equitum*. (1), BMNHL A5225; (3*a*, *b*), BMNHL A5216; (3*c*), NMM Q.102.F25; (6) BMNHL A5219; (9*a*), NMM F.22; (9*b*), NMM F.22 (above), BMNHL A5812 (below); (12), BMNHL A5810; 4, 7, 10, 13, Whooper Swan.

Fig. 1. Ulna, caudal aspect showing papillae remigiales caudales (R).

Figs. 2–4. Carpometacarpus. *a*, cranial aspect showing proximal articulatory surface (S). *b*, dorsal aspect showing proc. extensorius of os metacarp. alulare (T) and trochlea carpalis (U). *c*, caudal aspect showing papillae remigiales caudales (V).

Figs. 5–7. Phalanx proximalis digiti majoris. 5, 6*a*, 7, dorsal surface; 6*b*, distal view, showing ridge (W).

Figs. 8–10. Femur. *a*, cranial. *b*, caudal surface showing trochlea fibularis (X) and condylus lateralis (Y).

Figs. 11–13. Tarsometatarsus, showing proximodistal swelling (Z) on the trochlear groove of metatarsal IV.

All magn. × 1.

PLATE 70

R

2a

3a

S

4a

U

T

4b

3b

2b

1

5

6a

V

3c

W

6b

W

7

8a

9a

50 A

F.22

10a

8b

9b

Z

11

12

13

Y X

10b

NORTHCOTE, goose, swan, and swan-goose

TABLE 1. Mean limb-bone measurements (mm) of *equitum*, Greylag Geese, and extant Palaearctic swans. Measurements are given in appendices 1 and 2.

	n	equitum	n	Greylag Geese	n	Whooper Swans	n	Bewick's Swans	n	Mute Swans
Humerus										
Max. length	2	197·15	6	169·37	28	275·5	8	233·3	33	290·9
Min. shaft width	2	9·60	6	9·38	28	12·30	8	10·91	33	12·29
Ulna										
Max. length	2	*c.* 187	7	152·77	25	259·7	8	219·5	28	257·3
Min. shaft width	2	7·80	7	7·86	25	10·16	8	8·79	28	9·80
Carpomet.										
Max. length	4	91·18	5	96·44	17	137·47	2	118·90	9	133·36
Max. dorso-ventral width met. majus.	4	7·95	5	5·66	17	8·16	2	6·20	9	7·67
Phalanx										
Max. length	9	33·42	2	43·40	16	58·29	2	51·15	5	51·42
Femur										
Max. length	1	*c.* 79	5	80·16	26	108·78	8	94·33	34	104·67
Min. shaft width	1	9·90	6	7·52	26	10·46	8	9·39	34	10·20
Tarsomet.										
Min. shaft width	1	6·61	3	5·80	20	8·24	5	7·60	23	8·40

TABLE 2. Verheyen's (1955) osteometric indices applied to *equitum*, Greylag Geese, Whooper and Mute Swans.

| Index	equitum[1]	Greylag Geese[2]	Whooper Swans[2]	Mute Swans[2]
Humerus : ulna	*c.* 1·05	1·05–1·10	0·99–1·09	1·00–1·17
Humerus : carpomet.	2·16	1·73–1·77	1·88–2·08	1·95–2·32
Wing index (ulna + carpomet. : humerus)	*c.* 1·41	1·47–1·51	1·41–1·53	1·31–1·46
Femur : humerus	*c.* 0·40	0·47–0·49	0·38–0·42	0·34–0·37

[1] From Table 1.
[2] From appendix 2 and Verheyen (1955). These indices cannot be compared statistically since Verheyen published no raw data.

carpometacarpus of *equitum*, Greylag Geese, Whooper and Mute Swans confirm Bate's (1916) opinion that the *equitum* carpometacarpus is, first, very much 'stouter' than extant geese or swans—significantly 'stouter' than Whooper Swans ($P < 0.001$) and therefore, of Greylags and Mute Swans that are less 'stout' than Whooper Swans—and secondly, closer in proportion to Whooper than Mute Swans. Ratio (width : length) of the composite *equitum* femur shows it is 'stouter' (ratio $\approx$ 0·127) than in Greylag Geese (0·094) and Whooper and Mute Swans (0·096 and 0·097, respectively).

Ratios of limb-bone lengths

A ratio diagram (text-fig. 2) comparing bone lengths in Greylag Geese, Whooper and Mute Swans with *equitum* shows that the ratios for the goose deviate from *equitum* more than for the swans. Four osteometric indices used by Verheyen (1955) to characterize Greylag Geese, Whooper and Mute Swans are applicable (Table 2). The index (humerus : ulna) for *equitum* is within the ranges for Greylag Geese and the swans. The index (humerus : carpometacarpus) for *equitum* is greater than ranges for Greylag Geese and Whooper Swans but within that for Mute Swans. (Bate, 1916, p. 427 considered the *equitum* carpometacarpus 'relatively very much shorter' than in recent swans.) The wing index (ulna + carpometacarpus : humerus) for *equitum* is less than for Greylag Geese, but within the ranges for the swans. The index (femur : humerus) for *equitum* is less than
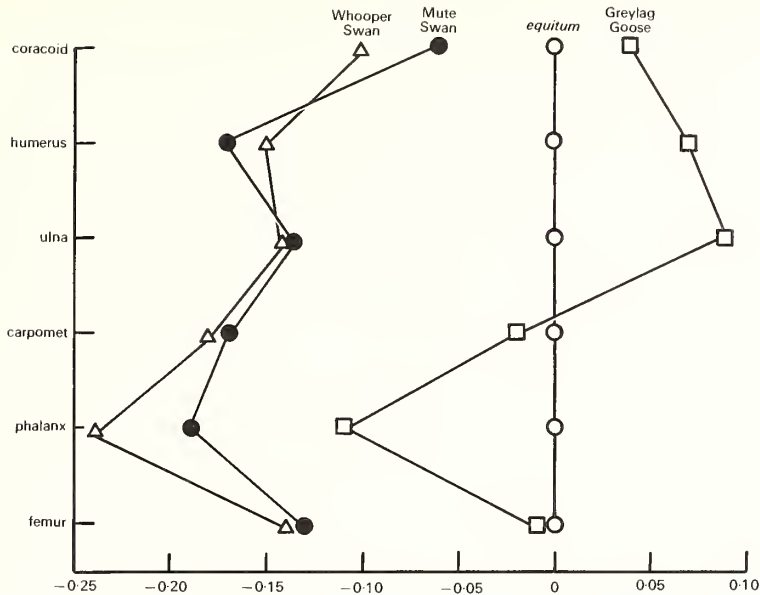
TEXT-FIG. 2. Simpson's ratio diagram comparing mean lengths for six bones of Greylag Geese, Whooper and Mute Swans, and *equitum*. The horizontal scale represents the deviation from *equitum* (the standard) of the logarithm of each dimension. No vertical scale is used. Though the line for no recent species lies exactly parallel to the one for *equitum*, which is straight, those for the swans are straighter than that for the goose. The relative proportions of *equitum* are, therefore, more like the swans than the goose.

for Greylag Geese, but greater than for Mute Swans; it is within that for Whooper Swans. For *equitum*, the index (chief phalanx : carpometacarpus) (0·37) is less than that for Greylag Geese, Whooper and Mute Swans (0·45, 0·42, and 0·39, respectively). The phalanx proximalis digiti majoris is significantly shorter in relation to the carpometacarpus in *equitum* than in Whooper Swans ($P < 0.001$) and hence Greylag Geese but this ratio is not significantly different from Mute Swans ($P = 0.6–0.7$).

DISCUSSION AND CONCLUSIONS

Genus and Species

Bate (1916) was correct in assigning the Maltese fossils to *Cygnus*. The comparatively longer beak and characteristic form of the scapula and coracoid, humerus head, carpometacarpus, and proximal phalanx of the major wing digit, 'stoutness' of the limb bones, and ratios of their lengths to one another all show *equitum* to be less like geese than swans. So far, there is little contrary evidence; only one feature on the proximal humerus, and one each on distal femur and tarsometatarsus. Brodkorb (1964) assigned the bird erroneously to *Anser* on account of the small size of the type specimens relative to extant swans, and Bate's (1916) figures of the proximal humerus (a paratype) and carpometacarpus (holotype).

Greater affinity between the extinct swan and *C. cygnus* than *C. olor* is indicated by the absence of a bony bill knob, two features proximally on the humerus, and perhaps the proportions of coracoid and humerus, and the relationship between femur and humerus lengths. However, the relative shortness of the chief wing phalanx and carpometacarpus is more similar to *C. olor*. This last character, combined with greater 'stoutness' of carpometacarpus and femur (and perhaps

TABLE 3. Estimation of weight (kg) of *Cygnus equitum*. Bone measurements from Table 1. Extant swan weights calculated from data given by Scott et al. 1972.

Formulae	Constants (K) for							
	Whooper Swans[1] using		Bewick's Swans[2] using		Mute Swans[3] Estimated wt. using		C. equitum	
	Femur	Humerus	Femur	Humerus	Femur	Humerus	Femur	Humerus
General								
Geometric similarity								
Length = $K_1 \times$ wt.$^{0.33}$ (Alexander 1971)	51·31	129·95	6·33	5·89	8·67	11·49	3·56	3·54
Diameter = $K_2 \times$ wt.$^{0.33}$ (Alexander 1971)	—	5·80	—	6·78	—	9·73	—	4·60
Elastic similarity								
Length = $K_3 \times$ wt.$^{0.25}$ (McMahon 1973, 1975)	61·46	155·65	5·55	5·05	8·41	12·20	2·59	2·57
Diameter = $K_4 \times$ wt.$^{0.375}$ (McMahon 1973, 1975)	—	5·23	—	7·10	—	9·76	—	5·05
For flying birds								
Femur length = $K_5 \times$ wt.$^{0.37}$ (Alexander 1983)	46·89	—	6·61	—	8·76	—	3·96	—

Actual weights:
1 9.72, n = 10.
2 6.05, n = 19.
3 10.63, n = 63.
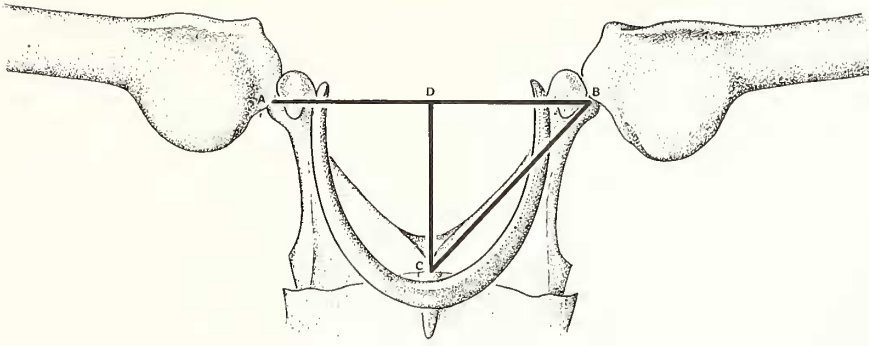
TEXT-FIG. 3. Estimation of distance between caputi humeri. AB joins articulation points of the caputi humeri with the facies artic. humeralis of the coracoids. In Anserini the anguli medialis of the coracoids meet (but do not overlap, Beddard 1898) at the spina externa of the sternum (C). D is the mid-point of AB. CD is perpendicular to AB. CD = $\frac{1}{2}$ AB. AC = BC = the hypoteneuse of a right-angled isoseles triangle. Therefore, $AC^2 = BC^2 = CD^2 + (\frac{1}{2}AB)^2 = 2 (\frac{1}{2}AB)^2$. For *Cygnus equitum* mean AC = mean BC $\approx$ 56 mm, $n = 4$. Thus AB, the width between the caputi humeri = $2\sqrt{56^2/2} \approx 79$ mm.

ulna), shorter limb-bone lengths, and distal humerus structure are diagnostic of the extinct bird; they justify Bate's (1916) designation of it as *sp. nov.*

Shape and size

Though *C. equitum* had the general shape of a swan, especially Whooper and Bewick's, its wings were probably more 'elliptical', that is, more highly cambered, with a low aspect ratio (length : width); greater 'stoutness' of the carpometacarpus, and probably of the ulna, suggests a thicker leading edge, and relative shortness of the hand bones suggest a lower aspect ratio. Though *C. equitum* was smaller than other swans (Table 1), its coracoids are comparatively long (length = 74·7 mm for *C. equitum* and for Bewick's Swan UMZC P6), so its body was comparatively broad.

Weight

Humerus diameter : length (see earlier) and femur : humerus length (Table 2) are the same in the extinct bird and in Whooper Swans, so weights of Bewick's and Mute Swans and *C. equitum* are estimated from scaling formulae using these measurements and constants calculated using Whooper Swans (Table 3). The formulae for geometric similarity give the closest estimates for Bewick's Swans. (Estimated weights of Mute Swans, since they are a different species from Whooper, are less close.) Using this formula, and femur and humerus lengths (the best parameters), mean weight of *C. equitum* $\approx$ 3·55 kg. Though within ranges for the largest geese, Greylag Geese, and the smallest swans, Bewick's Swans, 2·16–4·56 kg and 3·40–7·80 kg, respectively (Cramp and Simmons 1977), it is less than the mean weight for Bewick's Swans (6·05 kg from data given by Scott *et al.* 1972). At approximately 3·5–4·0 kg, *C. equitum* is the smallest known swan.

Wing span

Feathered wing span for *C. equitum* was estimated using the wing-skeleton span and the weight. 1, wing-skeleton span = sum of wing-bone lengths (from Table 1) + width between caputi humeri ($\approx$ 79 mm, text-fig. 3). Wing structure is similar in *C. equitum* to that in the extant swans (see earlier) where the ratio (wing-skeleton span : feathered wing span) $\approx$ 0·7–0·8 (Table 4). Therefore,

TABLE 4. Data for estimation of wing span (mm) of *Cygnus equitum*.

Wing-skeleton span of *equitum* and extant Palaearctic swans

Mean wing-bone lengths (mm) × 2 using Table 1

	Distance between caputi humeri (mm) (approx.)	humerus	ulna[1]	carpomet.	Digitus major phalanx[2]		Wing-skeleton span (approx.)	Feathered wing span (Cramp and Simmons 1977) (mm)	Ratio (wing-skeleton span : feathered wing span)
					proximal	distal (approx.)			
C. equitum	c. 79[3]	394·3	c. 374	182·36	66·84	56·8[4]	1155	—	—
Whooper Swan	101	551·0	519·4	274·94	116·58	94	1657	2180–2430	0·68–0·76
Bewick's Swan	92	466·6	439·0	237·80	102·30	76	1414	1800–2110	0·67–0·79
Mute Swan	105	581·8	514·6	266·72	102·84	87	1658	2080–2380	0·70–0·80

[1] Measurement of os carpi ulnari omitted.
[2] Digitus major has three phalanges in Anatidae (Baumel 1979, p. 155) but the relative length of the terminal phalanx is negligible.
[3] Calculated (see text).
[4] Calculated using ratio (distal : proximal phalanx) for Mute Swans (see text) = 0·85.

wing span for *C. equitum* ≈ 1·44–1·65 m (Table 4). 2, for all birds, wing span = $1.1 \times weight^{0.33}$ (Tucker 1977). Using estimated weights of *C. equitum* (Table 3), its wing span = 1·50–1·78 m, mean ≈ 1·68 m. For swans, wing span = a constant × weight $^{0.39}$ (Alexander 1971). Wing span of *C. equitum* = 1·30–1·88 m, 1·29–1·96 m, or 1·20–1·78 m, corresponding respectively to Whooper, Bewick's, or Mute Swans. The ratios (humerus : carpometacarpus) and (chief phalanx : carpometacarpus) in *equitum* are like Mute rather than Whooper Swans (see earlier), so the best estimate may be 1·20–1·78 m. In summary, the feathered wing span of *C. equitum* ≈ 1·44–1·65 m (using wing skeleton), 1·50–1·78 m, mean 1·68 m or 1·20–1·78 m (using scaling formulae).

Habitat and habit

Today Malta is relatively arid and bare, but remains of pygmy elephants and hippopotami, giant dormice, and land and freshwater turtles (Adams 1870, 1877), cranes (Lydekker 1890) of two species (Northcote 1982*b*, *c*, 1984, 1984–1985), geese (Parker 1865, 1869; Bate 1916), and two other swan species (Parker 1865, 1869; Northcote 1982*a*, 1981–1983) besides *C. equitum*, suggest that about 125 000 years ago there were stretches of fresh water and marshes besides that between Sicily and Malta (Northcote 1982*a*) and luxuriant vegetation including deciduous forest. The climate was probably warmer and moister than now as it was elsewhere in the Mediterranean according to Van der Hammen *et al.* (1971). Parker (1865, 1869) and Bate (1916) thought that foxes preyed on this fauna, though Falconer (1868) and Adams (1870) commented on the absence of carnivore bones from their Maltese excavations and Sondaar and Boekschoten (1967) and Sondaar (1971) considered that there were no large carnivores on Mediterranean islands in the Pleistocene. Zammit-Maempel (1982, p. 254) listed occurrences of bear remains on Malta but noted their sparcity and rarity.

No structural evidence supports Bate's (1916) statement that *C. equitum*, like some other island birds, was flightless. Its wings bore flight feathers, it was light enough to fly (the upper limit ≈ 12 kg, Pennycuick 1972) and there was no reduction of coracoid or wing bones in 'stoutness' or relative lengths. In addition, the ratio (length of crista pectoralis : humerus (i.e. insertion of the main flight muscles)) is similar in *equitum* (0·298) to Greylag Goose and Whooper Swan (approx. 0·300), indicating that it had fully formed flight muscles. (McGowan (1986), however, has shown the wing musculature of the flightless rail *Gallirallus australis* to be indistinguishable from *Fulica americana*, a fully flighted coot.) Characters of the proximal wing skeleton, as well as of the femur and tarsometatarsus indicate that *C. equitum* may have habitually taken off and alighted on level ground and was perhaps more terrestrial than extant swans. Taken together with the manœuvrability conferred by its smaller size, its more 'elliptical' wing shape, and perhaps its mode of elbow flexion, these factors suggest that *equitum* could live in such enclosed habitats as marshes, reed beds, and fen carr. *C. equitum* probably could not fly far because of its 'elliptical' wing shape and broad body (that are associated with slower flight, McFarland *et al.* 1979), together with wing-bone proportions less like the migratory Whooper and Bewick's Swans (that have tapered 'high speed' wings) than the relatively sedentary Mutes.

C. equitum occurred centrally on the island as well as in brackish and marine deposits (Brodkorb 1964). Evidently its large salt gland allowed it to eat plants from different areas. *C. equitum* was associated with the giant extinct swan *C. falconeri* Parker, 1865 and with Whooper Swan (Parker 1865, 1869; Bate 1916). Remains of the last named swan also occur in Devensian (Weichselian) as well as Ipswichian (Eemian) Interglacial deposits elsewhere in Europe (Lydekker 1891; Northcote 1979*b*), but the extinct dwarf and giant swans occur only in Interglacial deposits on Malta. Though able to forage on land, Whooper Swans eat mainly leaves, stems, and roots in shallow water (Cramp and Simmons 1977). Comparatively smaller herbivores tend toward a more selective browsing diet of higher calorific value (Prothero and Sereno 1982), so *C. equitum* probably ate mainly roots, shoots, flowers, fruits, and seeds on the water's edge. Comparatively larger herbivores nearly always eat food of lower calorific value (Prothero and Sereno 1982), so *C. falconeri*, an inland grazer (Northcote 1982*a*, 1981–1983), probably consumed a higher ratio of fibre to protein by cropping unselected grasses and whole plants on drier ground. Morphological differentiation,

by conferring ability to utilize different subniches, could thus have facilitated coexistence of the three swan species.

Evolution and extinction

The Maltese islands and Sicily are remnants of the land that emerged from the early Pliocene Mediterranean about five million years ago (Zammit-Maempel 1977). Ensuing Pleistocene climatic fluctuations facilitated rapid speciation (McFarland *et al.* 1979). During the 21 000 years of the last Interglacial, Siculo-Malta was isolated from mainland Italy by strong currents in the Straits of Messina (Sondaar and Boekschoten 1967). In both *C. equitum* and *C. falconeri* the change in size and assumption (or retention) of terrestrial, sedentary habits were probably adaptations to isolation in a mild climate, with plentiful food and rarity or absence of large carnivores.

In overall structure, both *C. equitum* and *C. falconeri* (Northcote 1982*a*, 1981–1983) differ from Mute, but resemble Whooper, Swans. Presumably, the actively flying Eurasian stock that, according to Johnsgard (1974), gave rise to *C. cygnus*, also produced *C. equitum* and *C. falconeri*. Terrestrial Anseriformes are more advanced than aquatic (Johnsgard 1965; Olson and Feduccia 1980), so that the terrestrial Whooper are more advanced than Mute Swans. *C. equitum* and *C. falconeri* were probably even more terrestrial than Whooper Swans. This characteristic, taken with their respective nanism and gigantism, indicates that both were even more advanced than Whooper Swans. However, the goose-like features and smaller size of *C. equitum* may be parallelisms or they may be primitive retentions, and so may the Mute-like hand proportions. In addition, remains of *C. equitum* chiefly represent fore-limbs, while those of *C. falconeri* are chiefly hind-limbs so that it is not possible to propose a more specific hypothesis of interrelationships.

Dwarf and giant swans probably evolved from separate invasions (maybe at different times) of ancestors derived on the mainland by allopatric speciation. It is unlikely that *C. equitum* and *C. falconeri* evolved sympatrically from, or in parallel with, intermediately sized swans such as Whooper Swans on Siculo-Malta because, as shown by Kondrashov and Mina (1986), an increased proportion of intermediates resulting from breeding with marginal populations would have prevented phenotypic separation of the marginals.

Rather rapid environmental changes accompanied the fall in temperature that terminated the Interglacial (Charlesworth 1957; Starkel 1977). Tectonic disturbances (Zammit-Maempel 1977) caused sea submergence of the area between Sicily and Malta and produced faulting, upthrowing, and tilting further south (Pedley 1981). Habitats were lost as a result of the sea-level changes and torrential rainfall eroded the sloping surfaces. These factors, combined with few, if any, large predators, may have led to overcrowding, overgrazing, and starvation. The less specialized Whooper Swans, migrants to Siculo-Malta, survived. The endemic *C. falconeri* and *C. equitum*, like many island bird species (Diamond 1981; McGowan 1986) may have been reluctant, rather than unable, to cross water.

REFERENCES

ADAMS, A. L. 1870. *Notes of a naturalist in the Nile Valley and Malta*, 117–187. Edmonton and Douglas, Edinburgh.

—— 1877. On gigantic land-tortoises and a small freshwater species from the ossiferous caverns of Malta, together with a list of their fossil fauna; and a note on chelonian remains from the rock-cavities of Gibraltar. *Q. Jl geol. Soc., Lond.* **33**, 177–191.

ALEXANDER, R. M. 1971. *Size and shape*. The Institute of Biology's Studies in Biology, **29**. Edward Arnold, London.

—— 1983. Allometry of the leg bones of moas (Dinornithes) and other birds. *J. Zool. Lond.* **200**, 215–231.

BATE, D. M. A. 1916. On a small collection of vertebrate remains from the Har Dalam cavern, Malta; with note on a new species of the genus *Cygnus*. *Proc. zool. Soc. Lond.* **28**, 421–430.

BAUMEL, J. J. 1979. Osteologia and Myologia. *In* BAUMEL, J. J., KING, A. S., LUCAS, A. M., BREAZILE, J. E. and EVANS, H. E. (eds.). *Nomina anatomica avium*, 53–123, 123–173. Academic Press, London.

BEDDARD, F. E. 1898. *The structure and classification of birds*. Longmans, Green and Co., London.

BELLAIRS, A. and JENKIN, C. R. 1960. The skeleton of birds. *In* MARSHALL, A. J. (ed.). *Biology and comparative physiology of birds*, **1**, Academic Press, London.

BOCK, W. J. 1962. The pneumatic fossa of the humerus in the passeres. *Auk*, **79**, 425–443.

BRODKORB, P. 1964. Catalogue of fossil birds. Part 2. Anseriformes through Galliformes. *Bull. Fla St. Mus. biol. Sci.* **8**, 195–335.

BROWN, R. H. J. 1963. The flight of birds. *Biol. Rev.* **38**, 460–489.

CHARLESWORTH, J. K. 1957. *The Quaternary Era, with special reference to its glaciation*. Arnold, London.

CRAMP, S. and SIMMONS, K. E. L. (eds.). 1977. *The birds of the Western Palearctic*, **1**, University Press, Oxford.

DE BRUIJN, H. 1966. On the Pleistocene Gliridae (Mammalia, Rodentia) from Malta and Mallorca. *Proc. K. ned. Akad. Wet.* B **69**, 480–496.

DELACOUR J. 1954. Systematic list and Introduction. *The waterfowl of the world*, **1**, 13–18. Country Life, London.

DESPOTT, G. 1928/1929. *Annual Report on the Working of the Museum Department during 1928–29*, S.VII–VIII. National Museum of Malta, Malta.

DIAMOND, J. M. 1981. Flightlessness and fear of flying in island species. *Nature*, **293**, 507–508.

FALCONER, H. 1868. IV. On the fossil remains of *Elephas meliteusis* an extinct pigmy species of elephant; and of other Mammalia, etc., from the ossiferous caves of Malta. *Palaeont. Mem. Falconer*, **2**, 292–308.

GASCOYNE, M., SCHWARCZ, H. P. and FORD, D. C. 1983. Uranium-series ages of speleothem from northwest England; correlation with Quaternary climate. *Phil. Trans. R. Soc. Lond.* B **301**, 143–164.

GEORGE, J. C. and BERGER, A. J. 1966. *Avian myology*. Academic Press, London and New York.

HOLMES, W. N. and PHILLIPS, J. G. 1985. The avian salt gland. *Biol. Rev.* **60**, 213–256.

HOWARD, H. 1964. Fossil Anseriformes. *In* DELACOUR, J. (ed.). *The waterfowl of the world*, **4**, 233–326. Country Life, London.

JOHNSGARD, P. A. 1965. *Handbook of waterfowl behaviour*. Constable and Co., Ltd, London.

—— 1974. The taxonomy and relationships of the northern swans. *Wildfowl*, **25**, 155–160.

KONDRASHOV, A. S. and MINA, M. V. 1986. Sympatric speciation: when is it possible? *Biol. Jl Linn. Soc.* **27**, 201–223.

KUHRY, B. and MARCUS, L. F. 1977. Bivariate linear models in biometry. *Syst. Zool.* **26**, 201–209.

LAMBRECHT, K. 1931. *Cygnopterus* und *Cygnavus*, zwei fossile schwäne aus dem Tertiär Europas. *Bull. Mus. R. Hist. nat. Belg.* **7**, 1–6.

—— 1933. *Handbuch der Palaeornithologie*. Borntraeger, Berlin.

LYDEKKER, R. 1890. On the remains of some large extinct birds from the cavern-deposits of Malta. *Proc. zool. Soc. Lond.* **28**, 403–411.

—— 1891. *Catalogue of the fossil birds in the British Museum (Natural History)*. British Museum (Natural History), London.

MCFARLAND, W. N., POUGH, F. H., CADE, T. J. and HEISER, J. B. 1979. *Vertebrate life*. Macmillan, New York.

MCGOWAN, C. 1986. The wing musculature of the Weka (*Gallirallus australis*), a flightless rail endemic to New Zealand. *Jl Zool., Lond.* **210**, 305–346.

MCMAHON, T. A. 1973. Size and shape in biology. *Science*, **179**, 1201–1204.

—— 1975. Using body size to understand the structural design of animals; quadrupedal locomotion. *J. appl. Physiol.* **39**, 619–627.

NORTHCOTE, E. M. 1979a. Determination of age and sex of long bones of Mute Swan *Cygnus olor*. *Ibis*, **121**, 74–80.

—— 1979b. Comparative and historical studies of European Quaternary swans and other aquatic birds. Ph.D. thesis (unpublished), University of Cambridge.

—— 1981. Differences in weight and habit of Whooper *Cygnus cygnus cygnus* and Mute *C. olor* swans in relation to differences in their long bones. *Bull. Br. Orn. Club*, **101**, 266–267.

—— 1982a. Size, form and habit of the extinct Maltese Swan *Cygnus falconeri*. *Ibis*, **124**, 148–159.

—— 1982b. The extinct Maltese Crane *Grus melitensis*. *Ibis*, **124**, 76–80.

NORTHCOTE, E. M. 1982c. Sympatry of Common Cranes *Grus grus* with larger cranes in the last *c.* 125 000 years. *Bull. Br. Orn. Club*, **102**, 141–142.

—— 1981–1983. The giant Maltese Swan. *Il-Merill*, **22**, 6–8.

—— 1984. Crane *Grus* fossils from the Maltese Pleistocene. *Palaeontology*, **27**, 729–735.

—— 1984–1985. The giant Maltese crane. *Il-Merill*, **23**, 1–4.

OLSON, S. L. and FEDUCCIA, A. 1980. *Presbyornis* and the origin of the Anseriformes (Aves; Charadriomorphae). *Smithson Contr. Zool.* **323**, 1–24.

PARKER, W. K. 1865. Preliminary notes on some fossil birds from the Zebbug Cave, Malta. *Proc. zool. Soc. Lond.* **1865**, 752–753.

—— 1869. On some fossil birds from the Zebbug Cave, Malta. *Trans. zool. Soc. Lond.* **6**, 119–124.

PEDLEY, H. M. 1981. Quaternary sediments, Malta. *In* BOSENCE, D. W. J., PEDLEY, H. M. and ROSE, E. P. F. (eds.). *Field guide to the Mid-Tertiary carbonate facies of the Maltese Islands*, 71–80. Palaeontological Association, London.

PENNYCUICK, C. J. 1972. *Animal flight*. Arnold, London.

PROTHERO, D. R. and SERENO, P. C. 1982. Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain. *Paleobiology*, **8**, 16–30.

SCOTT, K. M. 1983. Prediction of body weight of fossil Artiodactyla. *Zool. Jl Linn. Soc.* **77**, 199–215.

SCOTT, P. and THE WILDFOWL TRUST, SLIMBRIDGE (eds.). 1972. *The swans*. Michael Joseph, London.

SHUFELDT, R. W. 1909. Osteology of birds. *Bull. NY Mus.* **130**, 1–38.

SIMPSON, G. G., ROE, A. and LEWONTIN, R. C. 1960. *Quantitative zoology*. Harcourt, Brace and World, United States.

SONDAAR, P. Y. 1971. Paleozoogeography of the Pleistocene mammals from the Aegean. *In* STRID, A. (ed.). *Evolution in the Aegean*. Opera Botanica, **30**, 65–70.

—— and BOEKSCHOTEN, G. J. 1967. Quaternary mammals in the South Aegean Island Arc; with notes on other fossil mammals from the coastal regions of the Mediterranean. *Proc. K. ned. Akad. Wet.* B **70**, 565–576.

STARKEL, L. 1977. The palaeogeography of mid- and east Europe during the last cold stage, with west European comparisons. *Phil. Trans. R. Soc. Lond.* B **280**, 351–372.

STEJNEGER, L. 1882. Outlines of a monograph of the Cygninae. *Proc. US natn. Mus.* **5**, 174–221.

SY, M. 1936. Funktionell-anatomische Untersuchungen am Vogelflügel. *Jl Orn., Lpz.* **84**, 199–296.

TUCKER, V. A. 1977. Scaling and avian flight. *In* PEDLEY, T. J. (ed.). *Scale effects in animal locomotion*, 497–509. Academic Press, London.

VANDEN BERGE, J. C. 1979. Myologia. *In* BAUMEL, J. J., KING, A. S., LUCAS, A. M., BREAZILE, J. E. and EVANS, H. E. (eds.). *Nomina anatomica avium*, 175–219. Academic Press, London.

VAN DER HAMMEN, T., WIJMSTRA, T. A. and ZAGWIJN, W. H. 1971. The floral record of the late Cenozoic of Europe. *In* TUREKIAN, K. K. (ed.). *The Late Cenozoic Glacial Ages*, 391–424. Yale University Press, Newhaven and London.

VERHEYEN, R. 1953. Bijdrage tot de Osteologie en de Systematik van der Anseriformes. *Le Gerfaut*, **43**, 373–497.

—— 1955. La systématique des Ansériformes basée sur l'osteologie comparée. *Bull. Inst. R. Sci. nat. Belg.* **31 (35)**, 1–18; **(36)**, 1–16; **(37)**, 1–22; **(38)**, 1–16.

WOOLFENDEN, G. E. 1961. Postcranial osteology of the waterfowl. *Bull. Fla St. Mus. biol. Sci.* **6**, 1–129.

ZAMMIT-MAEMPEL, G. 1977. *An outline of Maltese geology*. Progress Press, Malta.

—— 1982. A Maltese Pleistocene sequence capped by volcanic tufa. *Atti. Soc. Tosc. Sci. nat. Mem.* A **88**, 243–260.

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